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Dinosaurs in decline tens of millions of years before their final extinction

Short title: Long-term decline of dinosaurs

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Abstract

Whether dinosaurs were in a long-term decline, or whether they were reigning strong right up to their final disappearance at the Cretaceous-Paleogene (K-Pg) mass extinction event 66 million years ago (Ma), has been debated for decades with no clear resolution. The dispute has continued unresolved because of a lack of statistical rigor and appropriate evolutionary framework. Here, for the first time, we apply a Bayesian phylogenetic approach to model the evolutionary dynamics of speciation and extinction through time in Mesozoic dinosaurs, properly taking account of previously ignored statistical violations. We find overwhelming support for a long-term decline across all dinosaurs and within all three dinosaurian subclades, Ornithischia, Sauropodomorpha and Theropoda, where speciation rate slowed down through time and was ultimately exceeded by extinction rate tens of millions of years before the K-Pg boundary. The only exceptions to this general pattern are the morphologically specialized herbivores, the Hadrosauriformes and Ceratopsidae, which show rapid proliferations throughout the Late Cretaceous instead. Our results highlight that, despite some heterogeneity in speciation dynamics, dinosaurs showed a marked reduction in their ability to replace extinct species with new ones, making them vulnerable to extinction and unable to respond quickly to, and recover from, the final catastrophic event.

Significance Statement

Whether dinosaurs were in decline or not before their final extinction 66 million years ago has been debated for decades with no clear resolution. This dispute has not been resolved because of inappropriate data and methods. Here, for the first time, we apply a statistical approach that models changes in speciation and extinction through time. We find overwhelming support for a long-term decline across all dinosaurs and within all three major dinosaur groups. Our results highlight that dinosaurs showed a marked reduction in their ability to replace extinct species with new ones, making them vulnerable to extinction and unable to respond quickly to, and recover from, the final catastrophic event, 66 Myr ago.

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Introduction

Non-avian dinosaurs met their demise suddenly, coincident with the Chicxulub impact in Mexico around 66 Ma (14). However, whether or not there was any long-term trend towards declining diversity leading to the K-Pg boundary has been controversial and debated for decades (1-13). This longstanding dispute has been prolonged partly because of differences in fossil datasets from different parts of the world and difficulties in rock dating, but most importantly from methodological weaknesses – previous attempts have been non-phylogenetic and analyses were conducted on simple time-binned tabulated data resulting in a lack of statistical rigor (phylogenetic and temporal non-independence have not been considered) and did not truly investigate evolutionary dynamics such as speciation and extinction rates. In fact, patterns of speciation and extinction in dinosaurs have gone largely unstudied (but see (8)). Here, we study speciation dynamics (relationship between speciation and extinction rates) using an exclusively phylogenetic approach in a Bayesian framework.

If speciation and extinction rate were constant (but speciation higher), we would expect to see a linear increase through time in the logarithm of the number of speciation events along each path of a phylogenetic tree (linear; Fig. 1A; see Methods). If speciation rate decreased through time, but remained above extinction rate, then we would expect a curvilinear relationship (Fig. 1B, C). Such a relationship would reach an asymptote (speciation = extinction; Fig. 1B) and eventually turn down as extinction rate surpasses speciation during the evolutionary history of the clade (Fig. 1C). The latter would correspond to a long-term pre-K-Pg demise in the case of dinosaurs. The distinction between such evolutionary dynamics can only be made using phylogenies with taxa sampled through time.

Results and discussion

Using a phylogenetic generalized linear mixed model in a Bayesian framework (15) and three recent large comprehensive dinosaur phylogenies comprising respectively 420 taxa (8) and 614 taxa (two trees (16)) , we found that the data are significantly better explained by a model in which extinction rate exceeds

speciation rate from ~24 million years before the K-Pg boundary than the simpler alternative model (Fig. 2A; difference in DIC [ΔDIC] between linear and quadratic models > 11; Table S1). Our findings are qualitatively identical across all three trees and we report on results from one of the 614-taxon trees (16).

Since non-homogeneity in evolutionary rates is widespread and common in nature (17-19) and dinosaurs are diverse – from the bipedal, carnivorous theropods to the quadrupedal, megaherbivorous sauropods – we might expect to find different speciation dynamics in the different dinosaurian subclades. When, model parameters were estimated separately for each of the three main subclades, Ornithischia, Sauropodomorpha and Theropoda, the same general pattern as in the total Dinosauria model was recovered, but with extinction rates exceeding speciation rates earlier at 48-53 Myr before the K-Pg boundary (Fig. 2B; ΔDIC > 12; Table S1). Ornithischia here refers to non-hadrosauriform, non-ceratopsid ornithischians, as the two Cretaceous subclades, Hadrosauriformes and Ceratopsidae, show speciation patterns distinct from other ornithischians; Lloyd et al. (8) also identified significant diversification shifts at the base of these and comparable clades, i.e., Euhadrosauria (here Hadrosauriformes, SI) and Ceratopsidae. In line with this, these two subclades show no signs of speciation slowdowns or downturns (ΔDIC between linear and quadratic models > 5 in favour of the linear model; Table S1) (inset Figs 2B, 3). Thus the difference in the timing of the switch from slowdown to downturn in the Dinosauria model and for the three major clades is due to the non-homogeneity in speciation processes across dinosaurian groups. However, these two subclades combined only represent 14% of dinosaur species, and over time, dinosaurs overwhelmingly experienced a reduction in their capacity to replace extinct species with new ones – net speciation per Myr at the time dinosaurs went extinct (66 Ma) were significantly below zero (speciation rate < extinction rate; Fig. 3B) in the three major clades (Table S12) – and Hadrosauriformes and Ceratopsidae are the exceptions.

The most prominent downturn is seen in the sauropodomorphs, where speciation increases rapidly through the Triassic and Early Jurassic (an average of 0.137 speciation events for every Myr) till ~195 Ma when speciation rate starts to slow down, and extinction rate surpasses speciation rate at ~114 Ma

(Figs 2B, 3). Early sauropodomorph lineages are numerous but not long-lasting, and taxa that originated earlier in geological time are successively replaced by younger ones. The near extinction of the diplodocoids at the end of the Jurassic, 145 Ma, did not affect high speciation rates (Fig 3), and sauropodomorphs only begin their decline approximately 30 Myr into the Early Cretaceous (Fig 3). The subsequent originations of titanosaurian taxa were not nearly enough to compensate for the continuous loss of sauropods throughout the remainder of the Cretaceous.

Speciation in theropods follows a slower increase (~0.07 speciation events for every Myr) with an early onset of speciation slowdown from the Late Triassic ~215 Ma to the Early Cretaceous ~120 Ma when extinction rate exceeds speciation rate (Figs 2B, 3). Although Theropoda contains one of the most morphologically diverse dinosaurian clades, the coelurosaurs, which includes the giant carnivorous tyrannosaurs, parrot-like oviraptorosaurs, large pot-bellied therizinosaurs, ostrich-like ornithomimosaurs, small sickle-clawed dromaeosaurs, and birds, most of which are Cretaceous in age, they originated in the Early to Middle Jurassic (Fig. 3), much earlier than expected from apparent fossil occurrences (8). Clades appearing even earlier, e.g. ceratosaurs, megalosauroids and allosauroids, also persist into the Late Cretaceous, all of which might suggest that the theropod speciation pattern would be a classic 'early burst' or adaptive radiation type speciation (20) with long protracted branches (8), which corresponds to a speciation slowdown model. While our results do show an initial burst of speciation events and a gradual and prolonged slowdown, consistent with an early burst model, the fact that extinction rate surpasses speciation rate highlights a more complex process in theropods (Figs 2B, 3).

Since birds underwent a radiation in the Early Cretaceous after their appearance in the Middle to Late Jurassic, one might expect that their pattern of speciation would be distinct from that of non-avian theropods. However, when we allow separate coefficients (intercept, slope and quadratic terms) in our model to be estimated for birds and non-avian theropods, the resulting regression parameters were not significant: in other words, the speciation dynamics in Mesozoic birds are not distinct from those of non-avian theropods

(Tables S1-S10). This is in line with recent findings of a high, sustained rate of change, from the Late Triassic to Early Cretaceous in the entire theropod lineage leading to *Archaeopteryx*, and among the earliest birds (21, 22).

Ornithischians show a similar increase to theropods (~0.06 speciation events for every Myr) to ~192 Ma, followed by a slowdown to ~114 Ma at which point extinction rate exceeds speciation rate (Figs 2B, 3). Key morpho-functional features in oral food processing distinguish hadrosauriforms and ceratopsids from other ornithischians, permitting them to exploit major new food sources (23, 24). Whether these herbivores were exploiting the new, small fast-growing herbaceous angiosperms that became common and widespread as early as the Aptian-Albian (125-109 Ma) of the Early Cretaceous (25) is much debated. The powerful jaws and massive dental batteries of these herbivores might have been adapted to other, tougher non-angiosperm plant food, and they benefited from a new adaptive complex in food processing.

Our results showing high levels of speciation in hadrosauriforms and ceratopsids, while consistent with previous findings (8), seem to contradict more recent work that suggests these groups underwent a decline in morphological diversity during the last two stages of the Cretaceous of North America (13, 26). These dinosaur species are morphologically and ecologically (at least at the family level) conserved (27), with most of the derived characteristics concentrated in their crania (24). Speciation can be high in these groups in spite of the potentially low morphological diversity, because Cretaceous dinosaurs exhibited increased provincialism (28) (speciation arising from geographic isolation rather than sympatric niche partitioning), increased alpha diversity (many more species with subtly varying skulls, but identical postcrania, sharing the herbivorous ecospace in single localities), and changing taxonomic composition of stable ecological community structures (ecological niches remain constant but taxa filling those niches changed through time (27, 29)).

An ecological limit on speciation, or the filling of available niches (30, 31) is commonly invoked to explain speciation slowdowns. Members of the same clade are more likely to compete for similar if not the same ecological niche or portions of ecospace (32, 33), and the more numerous the number of contemporary lineages, the fewer the number of available niches. We tested such

an effect by including a measure of intra-clade niche competition – cladewise lineage diversity, or the number of contemporary branches (including internal branches) for each taxon - in the model (SI). However, we find that cladewise lineage diversity is not significantly associated with speciation, nor does it explain the observed downturn; physical restrictions such as geography or range sizes could be more important.

We can indirectly assess the influence of geography, such as segregation by geographic barriers (30), using Mesozoic eustatic sea level reconstructions (34) as an additional covariate in our models. Although various hypotheses have been proposed regarding the influence of sea level on biodiversity in dinosaurs (see (35)), the most compelling suggests that increasing sea level results in fragmentation of large landmasses and can alter geographical distributions of habitats. In turn, this can lead to geographical segregation, reproductive isolation and ultimately speciation (30). Our results, for the first time, support this hypothesis – we find a significant positive effect of sea level on speciation (ΔDIC [5-Group quadratic – 5-Group + sea level models] > 16; pMCMC < 0.001; Tables S1-10) – though the effect is small; for every meter increase in sea level, speciation events increased by 0.2-0.25%. Horner et al. (29) observed that the emergence of transitional morphotypes coincides with marine transgressions in Late Cretaceous rocks of western North America, consistent with our finding that rising sea levels induce speciation. Importantly, the inclusion of sea level in any of our models does not diminish the temporal decline in species proliferation, despite the substantial rise of sea levels worldwide by some 150-200 m throughout the Cretaceous (Tables S2-10).

While we cannot positively identify a causal mechanism for the speciation downturn in dinosaurs, there are a multitude of possible global phenomena that occurred during the Cretaceous Period – e.g., the continued breakup of the supercontinents Laurasia and Gondwana (limiting free movement and eventual para- or peripatric speciation), intense prolonged volcanism (36), climate change (37-39), fluctuations in sea levels (34, 40), and ecological interaction with rapidly expanding clades (41). In order to accurately identify causal mechanisms of Mesozoic dinosaurian demise, we recommend that future studies focus on a longer time period than just the last 10-20 Myr of the Cretaceous (4, 13, 42, 43).

In addition, our results highlight the importance of considering the expected increase in species number as clades expand and accounting for shared ancestry using phylogenetic approaches.

Our study represents the first explicitly phylogenetic statistical treatment of speciation dynamics in dinosaurs. Unlike previous non-phylogenetic attempts to study changes in dinosaur taxic diversity across geological time bins (8-10, 13, 35, 44, 45), our method is robust to sampling and other potentially confounding factors (Tables S1-10; SI), and can statistically detect decreases in net speciation, which is difficult if not impossible to establish using conventional methods. Further, by accounting for the effects of shared ancestry, we provide a more accurate picture of dinosaurian speciation dynamics than the simple summing of species records through time.

Our results demonstrate that dinosaurs were in decline for a much longer period of time than previously thought - extinction rate surpassed speciation rate at least 40 Myr before their final extinction. This prolonged demise leaves plenty of time for other animal groups to radiate and flourish as more and more ecological niches open up, most prominently the pre-K-Pg expansion of crown mammals (46). While Mesozoic dinosaurs undoubtedly dominated the terrestrial megafauna till the end of the Cretaceous, they did see a reduction in their capacity to replace extinct species with new ones, making them more susceptible to sudden and catastrophic environmental changes like those associated with the asteroid impact.

Materials and Methods

Phylogeny. We used three recent large comprehensive dinosaur phylogenies comprising respectively 420 taxa (8) and 614 taxa (two trees (16)). Trees were scaled according to the midpoint time of each terminal stratigraphic range (16) using the 'equal' scaling method (47) implemented in the paleotree R package (48). Additionally we scaled the trees using two alternative sets of terminal dates, the first appearance dates (FAD) and last appearance dates (LAD) to assess the effects of tree scaling on model results.

Generalized linear mixed models. We fitted generalized linear mixed models (GLMM) in a Bayesian framework through Markov-chain Monte Carlo (MCMC) using the MCMCglmm R package (15). The total number of speciation events (node count) along the phylogenetic path for each taxon was modeled as the response variable, with the corresponding path length (time elapsed from root to tip) as the main effects predictor variable - this model formulation forms the null linear model (Fig. 1A). We also fitted a speciation slowdown model, with the addition of a quadratic term ($time^2$) to the main effect. Incidentally, a quadratic model can also explain the opposite case, where speciation rate increases while extinction rate remains constant. We include phylogeny as a random effect in order to account for shared ancestry.

Separate intercepts, slopes and quadratic terms were estimated for the three major dinosaurian clades (Sauropodomorpha, Theropoda, Ornithischia) (3-Group model). Lloyd et al. (8) previously identified two significant diversification shifts in the Cretaceous ornithischians, at the base of the clades Euhadrosauria (here Hadrosauriformes) and Ceratopsidae, so we estimated separate model coefficients (intercepts and slopes) for these groups from other ornithischians (5-Group model).

Chains were run for 10^6 iterations, sampling at every 1000th iteration. We fitted a GLMM with a Poisson link to appropriately account for error structure in count data – although we discuss predicted curve shapes in log space, we did not log-transform node count for model fitting (49). MCMCglmm automatically accounts for overdispersion in the count data distribution. We used default priors (mu=0, $V=I\times10^{10}$ where I is an identity matrix) for the fixed effects and parameter expanded priors (V=1, nu=1, alpha.mu=0, $alpha.V=25^2$) for the phylogenetic random effects (15).

Model fit was assessed using Deviance Information Criterion (DIC) and inspection of model parameter significance (using p-MCMC: twice the proportion of the MCMC estimates that crosses zero). We determined the best fit model as the model with the lowest DIC score, and where the difference in DIC score compared with that of a base model (ΔDIC) is greater than 4. In the case where multiple models had non-significant differences in model fit (i.e., $\Delta DIC < 4$), we

inspected the significance of model parameters and selected the model with significant covariates (i.e., non-significant covariates were removed).

Extrinsic factors. As the fossil record has long been known to be incomplete (50, 51) – it is possible that the observed slowdown and downturn are by-products of undersampling. This would imply that there is a systematic downwards bias in the phylogeny towards recent times, which would be counter to the usual expectation for poor sampling (50, 51). Here, in order to test the effect of such biases, we fitted additional models with appropriate covariates, including stage-level formation counts (because formation count is widely reported to be associated with sampling bias) (9, 10, 12, 35, 44, 52, 53), taxon-specific formation counts (the number of formations in which a taxon is found), taxon-specific collection count (the number of fossil collections in which a taxon is represented), cladewise valid taxa counts (the known under-representation in the phylogeny) (54), fossil quality scores (state of preservation) (55) and body size (smaller taxa are less likely to be preserved) (56).

As an indirect measure of the influence of geography on speciation dynamics, such as segregation by geographic barriers (30), we used Mesozoic eustatic sea level reconstructions (34) as an additional covariate in our models (mean sea level value along each terminal branch). We also tested the ecological limit on clade diversification, or the possible effects of niche saturation, by adding a measure of intra-clade diversity taken as the number of contemporary branches (including internal branches) for each taxon (the number of tips in time-sliced trees (48)).

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Figures

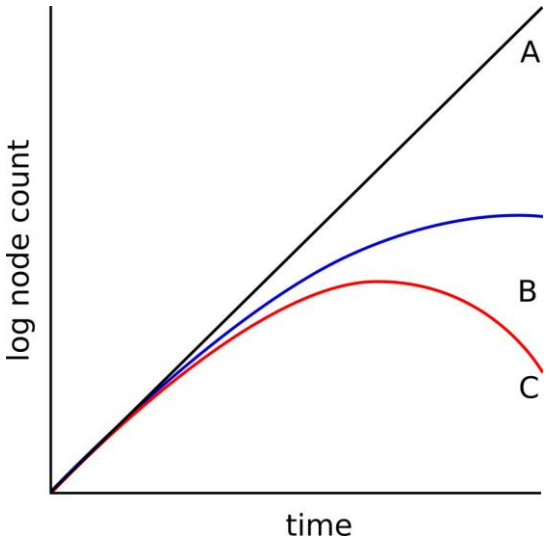

Fig. 1. Theoretical models of speciation through time

If speciation and extinction rate were constant through time (but speciation higher) in dinosaurian history, we would expect to see a linear increase through time in the logarithm of the number of speciation events along each path of a phylogenetic tree (A). If speciation rate decreased through time, but remained above extinction rate, then we would expect a curvilinear relationship (B, C). Such a relationship would reach an asymptote (speciation = extinction; B) and eventually turn down as extinction rate surpassed speciation during the evolutionary history of the clade (C). The latter would correspond to a long-term pre-K-Pg demise in the case of dinosaurs.

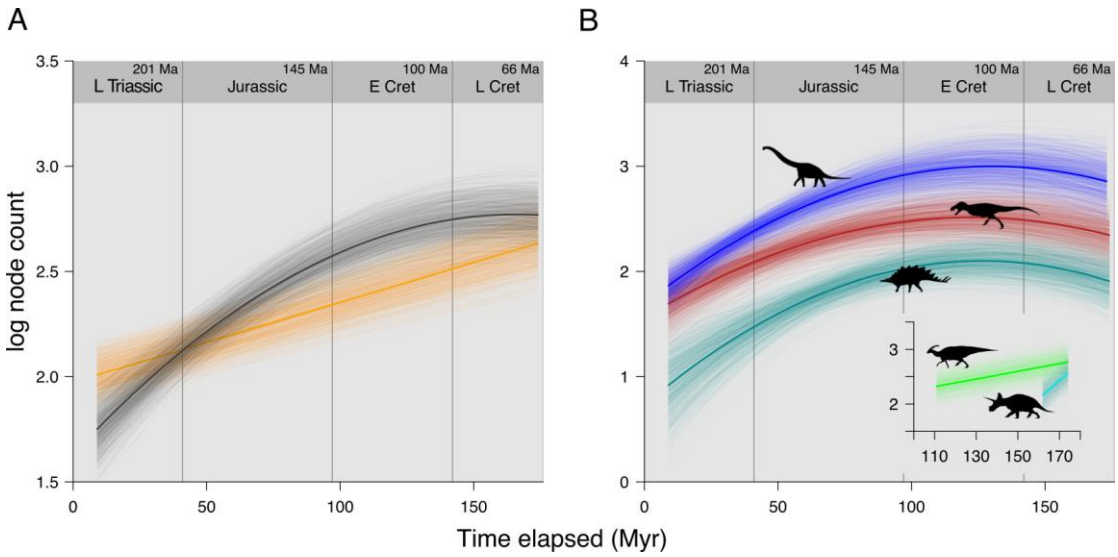

Fig. 2. Model predictions of speciation through time in Mesozoic dinosaurs

Compared with the linear model (orange), the quadratic model displaying a speciation slowdown substantially improves model fit (delta DIC > 4) (A). This pattern holds true in the three major clades, Ornithischia (green), Sauropodomorpha (blue) and Theropoda (red), and further improves model fit (B). Model fit significantly improves when separate model parameters are estimated for the ornithischian subclades Hadrosauriformes (light green) and Ceratopsidae (light blue) from other ornithischians (inset B), but the slowdown and downturn are not observed for the two Cretaceous ornithischian subclades. Posterior predictions (transparent lines) show the uncertainties in the model. Mean posterior values are in bold. Vertical lines indicate major stratigraphic boundaries (with their ages in Ma). Silhouettes from phylopic.org.

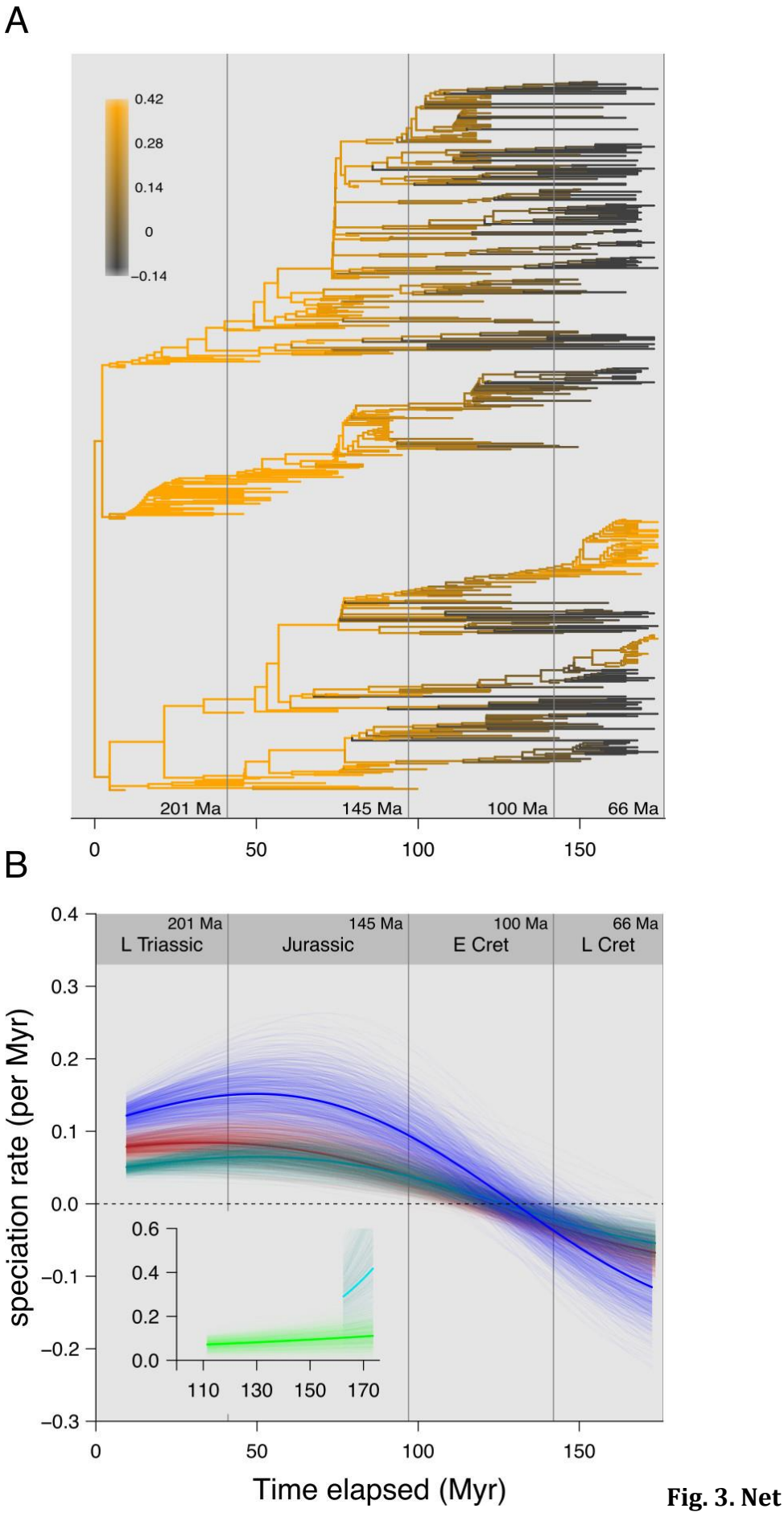
A
0.42
0.28
0.14
0
−0.14
201 Ma
145 Ma
100 Ma
66 Ma
0
50
100
150
B
201 Ma
145 Ma
100 Ma
66 Ma
L Triassic
Jurassic
E Cret
L Cret
0.4
0.3
0.2
0.1
0.0
−0.1
−0.2
−0.3
speciation rate (per Myr)
0.6
0.4
0.2
0.0
110
130
150
170
0
50
100
150
Time elapsed (Myr)

Fig. 3. Net

speciation per Myr through time in Mesozoic dinosaurs

Net speciation per Myr can be calculated from model predictions (Fig. 2B) as differences between intervals, here per 1 Myr. Each branch of a dinosaurian phylogeny was assigned a net speciation per Myr value based on its temporal location and group membership, and plotted on a colour gradient (A). Earlier branches have higher net speciation per Myr (orange) while later branches have lower net speciation per Myr (dark grey), except in Hadrosauriformes and Ceratopsidae, in which net speciation per Myr increase with time. The three major dinosaur groups, Sauropodomorpha (blue), Theropods (red), and non-hadrosauriform, non-ceratopsid Ornithischia (green), show an early onset of speciation slowdown (B), until the middle of the Early Cretaceous, when speciation rates are exceeded by extinction rate (net speciation per Myr fall below zero [dashed horizontal line]). Values above zero indicate increases in species counts, while those below zero indicate decreases in species counts. Hadrosauriforms (inset, light green) show a slow increase in net speciation per Myr through time, while ceratopsians (inset, light blue) show a highly variable, but on average, a rapid increase towards the end of the Cretaceous. Posterior predictions (transparent lines) show the uncertainties in the model. Mean posterior values are in bold. Vertical lines indicate major stratigraphic boundaries (with their ages in Ma) as in Fig. 2. Silhouettes from phylopic.org.